change (FELSENSTEIN, 1984). The tree shown has been optimized (from among the more than 8000 possible trees relating 10 samples) and *Ningbingia australis* has been designated the outgroup for purposes of rooting the tree.

We share with SWOFFORD & BERLOCHER (1987) the view that allozyme frequencies are evolutionarily meaningful and that traditional cladistic methods that reduce the data by "presence/absence" coding are inferior. For this reason, we have not used a Hennigian approach to the genetic data. It is still important to heed FELSENSTEIN's (1982) admonition not to adopt a single method for inferring evolutionary trees until much more is known about the biological assumptions and statistical behavior of the various approaches.

We will postpone a detailed discussion of the phenetic and phylogenetic trees presented here until more species are added to the analysis. Suffice to say, we are able to distinguish the various taxa and produce biologically realistic hypotheses concerning their relationships. All trees cluster the taxa in a similar manner affirming the genetic affinities between *Cristilabrum primum* and *C. grossum* and the greater differentiation of their congener, *C. monodon. Turgenitubulus* is seen to cluster with *Cristilabrum* rather than *Ningbingia.* On the basis of fundamentally divergent stimulatory structures in the terminal genitalia, Solem (in preparation) considers that *Ningbingia* and *Cristilabrum* are not closely related to each other. It may be that they will cluster more closely with genera from elsewhere in Australia than with each other. In contrast, *Turgenitubulus* and *Cristilabrum* are very closely related. Unique derived genital features of the former can be derived from the latter, and some species show partly intermediate stages (Solem, in preparation).

A comparison of the original descriptions of the 28 species (in the genera *Ningbingia, Turgenitubulus, Cristilabrum,* and *Ordtrachia*) of endemic camaenids (SOLEM, 1981, 1985, 1988b, 1989b) suggests that the reconstruction of a phylogeny based on a cladistic analysis of anatomical variation may not be possible (Solem, in preparation). Numerous apparent cases of parallel evolution, convergent evolution, and reversal occur among the continuous morphological variables studied. In contrast, the allozymic data appear suitable for rigorous phylogenetic analysis. In subsequent papers we will develop evolutionary hypotheses based on the inclusion of additional endemic species and representatives of possible ancestral outgroups. Again, available anatomical data do not immediately identify a probable sister group to the Ningbing endemics elsewhere in northwestern Australia. Thus, allozymes will be used to establish alternative hypotheses for testing.

ACKNOWLEDGMENTS

The initial field work and systematic study that led to this project has been supported by National Science Foundation grants DEB 75-20113, DEB 78-21444, DEB 81-19208, and BSR 85-00212 to Field Museum of Natural History. A separate NSF grant, BSR 8312408, to Field Museum of Natural History, enabled participation of K. C. Emberton in the field work and funded the electrophoretic work at the University of California, San Diego through a subcontract. We gratefully acknowledge this generous support.

For field assistance during several field trips to the Ningbing Ranges, we thank Carl C. Christensen, Laurel E. Keller, Laurie Price, Fred and Jan Aslin, Lucky Laurie, and K. C. Emberton. For assistance in expediting this project, we thank Victoria Huff, Margaret Baker, Beth Morris, and Linnea Lahlum of Field Museum of Natural History, and M. Patricia Carpenter at UCSD.

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The Veliger 33(2):140–144 (April 2, 1990)

THE VELIGER

Comparative Zoogeography of Marine Mollusks from Northern Australia, New Guinea, and Indonesia

by

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Abstract. The shallow-water marine prosobranch mollusks occurring in northern Australia are compared with species living in adjacent areas of the Indo-West Pacific (Indonesia and New Guinea) based on an analysis of the presence or absence in each of the three areas of 977 species from 21 families of prosobranch gastropods. The fauna of northern Australia, while diverse, is generally considered less diverse than that which occurs in the biogeographic center of the Indo-West Pacific, the area bordered by the Philippines, Malaysia, and New Guinea. In the present study 754 species are known to occur in northern Australia, 625 in Indonesia, and 809 in New Guinea. If Indonesia and New Guinea are combined, 876 species are known to occur in the islands to the north of Australia, 16% more species than in Australian waters. With our uncertain knowledge of the taxonomy and distributions of individual species, this difference is not considered to indicate a reduced diversity in the marine shallow-water fauna of northern Australia.

Almost 92% of the mollusks studied occur in Indonesia and/or New Guinea; just over 8% are endemic to northern Australia. Slightly higher percentages of endemism (13%) occur in the two other best known, taxonomically diverse groups, echinoderms and fish. These data suggest that as the fauna becomes better known the reasons for recognizing a separate Tropical Australian Province in the Indo-West Pacific will be further reduced.

INTRODUCTION

The northern coastline of the continent of Australia, from North West Cape in Western Australia to the southern limit of the Great Barrier Reef in Queensland, has a tropical shallow-water marine fauna that is closely related to that which occurs in the central Indo-West Pacific (EKMAN, 1967). Further south on both the east and west coasts of Australia the fauna is a mixture of a decreasing proportion of tropical species, an increasing proportion of temperate species, and a group of species endemic to either the east or west coast.

Early studies (HEDLEY, 1926; WHITLEY, 1932) divided the marine fauna of the north coast of Australia into three provinces separated at Cape York in northern Queensland: the Dampierian Province of northwestern Australia, the inshore Banksian Province of Queensland, and the Solanderian Province, which encompassed the Great Barrier Reef off the Queensland coast. ENDEAN (1957), working on echinoderms, combined the inshore (Banksian) region of Queensland and the Dampierian Province as a Tropical Australian Province across the entire north coast of the continent, but regarded the Great Barrier Reef as a distinct faunal region. As knowledge of the fauna of northwestern Australia improved several studies have concluded that there is no need to divide the coastline of northern Australia, and a single Tropical Australian Province which includes the Great Barrier Reef is recognized (WILSON & GILLETT, 1971; WELLS, 1980, 1986; WILSON & ALLEN, 1988).

The relationships of the tropical Australian coast to the traditional faunistic center of diversity in the Indo-West Pacific, the area bordered by a triangle connecting the Philippines, Malaysia, and Papua New Guinea (BRIGGS, 1975), are still uncertain. Northern Australia lies outside the triangle and while the fauna is diverse, it is not thought to equal the diversity of the central area (BRIGGS, 1975).

This paper has two goals: to examine faunal diversity in northern Australia to determine whether diversity is in fact less than in the traditional faunistic center of diversity and to examine the validity of separating northern Australia from the area to the north as a Tropical Australian Province.

[1] Publication No. 25 of the Christensen Research Institute, Madang Papua New Guinea.

MATERIALS AND METHODS

The same families of prosobranch gastropods examined in my previous papers (WELLS, 1980, 1986) are utilized for comparison. Gastropod species listed in previous papers from Western Australia (WELLS, 1980, 1986; WELLS & SLACK-SMITH, 1986), the works of HINTON (1972, 1978, 1980), WILSON & GILLETT (1971), ROBERTS *et al.* (1982), WELLS & BRYCE (1986), and SHORT & POTTER (1987), and the list of species I collected at Madang, Papua New Guinea, in 1987 were used to develop a composite list of species known to occur in the region. The collections of the Western Australian Museum (WAM) were searched to provide additional unpublished records. In addition to being strong in Western Australian material, the WAM collection has considerable Indonesian material collected during the Muriel King and Rumphius expeditions in the 1960s and 1970s. The literature was also examined for additional records; a complete list of reports used is included in the Literature Cited. Emphasis was placed on records from revisionary works such as REID (1986) and BRATCHER & CERNOHORSKY (1987) rather than more general works. Only records where a species was specifically listed from an area were used; distribution maps suggesting that the range of a species should include one of the three areas, but not specifying a locality, were disregarded. Additional records were provided by examining the collections of the Australian Museum, Sydney.

Species examined are all shallow-water animals that occur in depths of less than 50 m for at least part of their range. Species that occur only in deeper water are disregarded.

For the purposes of this paper the three geographic areas need to be defined. The paper is intended to compare the mollusks of three areas, but political boundaries do not always reflect zoogeographic regions. In addition some of the literature and specimen records list "Borneo" or "New Guinea" without specifying a more exact locality. Species included from northern Australia are those that have been recorded at some point from the area between North West Cape in Western Australia and the southern extremity of the Great Barrier Reef on the east coast. The continental shelf atolls of Rowley Shoals, Scott Reef, Seringapatam Reef, and Ashmore Reef off northern Western Australia and records from the Australian islands of Torres Strait are included. A small component (<5%) of the fauna of northern Australia consists of temperate and east and west coast endemic species that reach into the southern portions of the tropical areas; these have been ignored in the present paper. The Torres Strait islands belonging to Papua New Guinea and also New Britain Island are included in the New Guinea list. The New Guinea list covers all of the island of New Guinea, including the western half, which is the Indonesian province of Irian Jaya. The islands to the west of New Guinea and the remainder of the Indonesian Archipelago are included in Indonesia. Most of the island of Borneo is Indonesian, though the northern portion is part of Malaysia. For the purposes of this paper all records from Borneo are included in the Indonesia category.

An index of similarity (KREBS, 1978) was used to compare species overlap between the various areas. The formula is $I = \frac{2c}{a + b}$, where a is the number of species in area a, b the number in area b, and c the number of species in common. The index ranges from 0 if there are no species in common to 1 if the overlap is total.

RESULTS

A total of 977 prosobranch gastropod species in the 21 families were recorded in at least one of the three regions. The most diverse families are the Conidae with 127 species, Mitridae (109), Terebridae (94), Costellariidae (95), Cypraeidae (87), and Nassariidae (84). The high diversity in these families is probably not an artifact of collecting data, but is partly due to numerous records that have resulted from recent revisions by CERNOHORSKY (1976: Mitridae), CERNOHORSKY (1984: Nassariidae), and BRATCHER & CERNOHORSKY (1987: Terebridae) and shell books by WALLS (1980: Conidae); PECHAR *et al.* (1980: Mitridae and Costellariidae), and BURGESS (1985: Cypraeidae). Together the five families have 596 species, 61% of the total examined. Some of the families that are not popular with shell collectors and have not been recently revised are probably underrepresented. For example only 25 species of Trochidae are included. These are primarily species with large shells such as those of the genera *Trochus* and *Tectus*, but species with smaller shells such as *Clanculus* are not fully covered. For these reasons the diversity of the various families should be considered to be only relative. These problems are probably characteristic of all three areas, and although northern Australia is better collected than the others, the general trends should be valid. Most of the species occurred in more than one of the three areas: 474, or 48.5% in all three; 251, or 25.7% in two; 252, or 25.8% in only one area (Table 2).

There are 754 species in northern Australia compared to 625 for Indonesia and 809 for New Guinea (Table 1). Thus New Guinea has 7% more species than northern Australia, but 17% fewer species are known to occur in Indonesia. If northern Australia (754 species) is compared with New Guinea and Indonesia combined (876), New Guinea-Indonesia has only 122, or less than 16% more species than the northern Australian coastline.

Ninety-six of the species examined were recorded only from Australian waters, raising the possibility that they are endemic to tropical Australia. Thirty-three of these are known to occur in Indo-West Pacific areas elsewhere than Indonesia-New Guinea. These species may also be found in Indonesia-New Guinea, but no records could be located. Most of the remaining 63 species are probably Australian endemics; this indicates that a maximum of

Table 1

Number of shallow-water species of 21 families of gastropod mollusks recorded from three geographical areas. Abbreviations: AUS, northern Australia; NG, New Guinea; IND, Indonesia; TOT, total; ISL, islands (combination of New Guinea plus Indonesia); END, species possibly endemic to Australia.

Family	Number of species									
	AUS	NG	IND	TOT	AUS-NG	AUS-IND	NG-IND	ISL	AUS-ISL	END
Haliotidae	6	5	4	6	5	4	4	5	5	1
Trochidae	24	20	16	25	19	15	15	21	20	2
Turbinidae	17	13	12	20	12	9	9	16	13	2
Neritidae	10	8	10	10	8	10	8	10	10	0
Littorinidae	18	16	21	28	13	12	14	23	13	5
Strombidae	35	37	36	39	34	32	35	38	34	0
Naticidae	24	20	17	25	19	17	16	21	20	2
Cypraeidae	73	72	66	87	68	59	61	77	69	1
Cassidae	9	10	11	11	9	9	10	11	9	0
Tonnidae	9	10	6	11	8	6	5	11	9	0
Muricidae	44	38	21	53	30	18	18	41	32	8
Thaididae	43	35	36	44	35	36	29	42	42	1
Columbellidae	14	11	11	15	10	11	9	13	12	1
Nassariidae	50	57	47	84	40	38	46	78	44	4
Fasciolariidae	26	21	16	27	21	15	15	22	22	2
Olividae	23	30	27	35	21	19	24	33	21	1
Mitridae	83	102	69	109	77	56	56	105	79	2
Costellariidae	59	93	43	95	57	35	43	93	57	1
Volutidae	28	8	9	32	6	7	3	14	10	21
Conidae	93	108	87	127	81	70	74	117	85	5
Terebridae	66	65	60	94	52	42	40	85	57	4
Totals	754	809	625	977	625	520	534	876	663	63

8.3% are endemics. Of the 63 species, 21, or one-third are volutes (Table 1).

DISCUSSION

The data presented above once again demonstrate, at least for mollusks, the close affinity between the shallow-water marine fauna of the coastline of northern Australia and the adjacent areas (Indonesia and New Guinea) of the Indo-West Pacific. The great majority (74%) of the species examined are known to occur in more than one of the three areas analyzed. All of the authors of zoogeographical papers examined (Clark, 1946; Endean, 1957; Knox, 1963, 1980; Briggs, 1975; Marsh, 1976; Wilson & Stevenson, 1977; Wells, 1980, 1986; Marsh & Marshall, 1983) agree that the marine shallow-water fauna of northern Australia is part of the Indo-West Pacific.

The close relationship between the fauna of northern Australia and the islands to the north is not surprising. A full range of marine shallow-water habitats is in the two areas, including mangroves, coral reefs, rocky and sandy intertidal and subtidal areas, and estuaries. The ocean is shallow between Australia and New Guinea and Indonesia, with land bridges existing during several periods of lowered sea levels during the Pleistocene. The most recent time during which there was a land bridge across Torres Strait was between 8000 and 6000 years BP (Marsh & Marshall, 1983). Even today, with Australia separated by oceanic waters from Indonesia and New Guinea, a series of islands allows ready distribution between areas by species with planktonic larval stages.

Two questions remain to be addressed: is the fauna of northern Australia less diverse than that of the faunistic center of the central Indo-West Pacific (the Philippines-Malaysia-New Guinea triangle of Briggs [1975]) and is the fauna of northern Australia sufficiently distinct to be regarded as a separate zoogeographical province?

For the 21 families of prosobranch gastropods examined the total number of species known to occur in Indonesia-New Guinea is 16% greater than those known to live in northern Australia. Two problems arise in evaluating this figure. First, the data cannot be statistically tested. However, the figure of 16% itself is not substantial. I know of no other quantitative comparison, either in mollusks or other groups, of the fauna of northern Australia with the adjacent areas of the Indo-West Pacific to which the figure can be compared. The second problem is that the data are obviously incomplete—further collecting in all of the three areas will undoubtedly reveal new records. Most of the families have not recently been revised, and future revisions will change our concepts of at least some of the species involved, perhaps resulting in the synonymizing of some